

Lugworm (*Abarenicola affinis*) in seagrass and unvegetated habitats

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Abstract In Otago, southern New Zealand, the lugworm *Abarenicola affinis* resides in neighbouring tidal inlets with and without seagrass (*Zostera muelleri*). A comparison of abundance, body size and biomass of *A. affinis* between seagrass habitat (Papanui Inlet) and unvegetated habitat (Hoopers Inlet) showed little seasonal variation of these parameters in each habitat and relatively similar abundances between both habitats. In contrast, lugworm biomass was considerably lower in the seagrass habitat due to the lack of large individuals compared with unvegetated habitat. In the seagrass habitat, there was a significant negative influence of *Z. muelleri* below-ground biomass on abundance and biomass of *A. affinis*, indicating that seagrass affected lugworm burrowing and/or feeding processes. In contrast to the unvegetated habitat, where lugworms spread relatively evenly across the intertidal area, lugworms were mostly restricted to the upper intertidal zone in the seagrass habitat. The findings suggest that the extensive seagrass bed in the mid and low intertidal zones of Papanui Inlet limited lugworm distribution in an otherwise suitable habitat. Whereas small lugworms colonised seagrass areas, the largest individuals occurred only in unvegetated sediment and seemed to be more hampered

by the presence of seagrass than smaller individuals. The findings highlight negative feedback between antagonistic ecosystem engineers, with the potential of seagrass physical structures (autogenic engineering) to impact negatively on lugworm activity (allogenic engineering).

Keywords *Abarenicola affinis* · *Zostera muelleri* · Lugworm habitat comparison · Tidal inlets · Species interactions · Ecosystem engineers · Negative feedback

Introduction

In coastal sediments, habitat modifying organisms that alter sediment properties and dynamics have a strong influence on the distribution and abundance of other benthic biota (e.g. Reise 2002; Bostroem et al. 2006; Berkenbusch and Rowden 2007; Eriksson et al. 2010). These organisms represent examples within the concept of ecosystem engineering, which is used to describe species that directly or indirectly modify habitat resource flow by causing state changes in the biotic and abiotic environment (Jones et al. 1994). Two types of ecosystem engineers can be distinguished: autogenic engineers modify habitats via their own physical structure, whereas allogenic engineers modify habitats via their activity (Jones et al. 1994). Many recent studies have focussed on the role of benthic ecosystem engineering in intertidal soft-sediments, which are particularly amenable to habitat modifications (e.g. Berkenbusch and Rowden 2003; Bos et al. 2007; Volkenborn et al. 2007; Ekloef et al. 2011). In these habitats, autogenic and allogenic ecosystem engineers generate complex networks of species interactions, mediated by the transformed sediment matrix (Reise 2002; Bouma et al. 2009).

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Two notable examples of autogenic and allogenic ecosystem engineers on tidal flats are seagrasses and bioturbating lugworms, respectively (Bouma et al. 2009). Both seagrasses and lugworms modify habitats to their own benefit and have the potential to inhibit the distribution and functioning of each other, when co-existing on tidal flats (van der Heide et al. 2007; van Wesenbeeck et al. 2007; Bouma et al. 2009; Ekloef et al. 2011). Sediment processing by lugworms can lead to burial of seagrass seeds and plants, whereas, in turn, established root systems of seagrasses consolidate the sediment, inhibiting reworking and burrowing activities of lugworms (Brenchley 1982; van Wesenbeeck et al. 2007; Valdemarsen et al. 2010; Ekloef et al. 2011).

In view of their ecological significance, lugworm populations have been widely studied, with most research focussing on *Arenicola marina*, which occurs on the often extensive and relatively homogeneous tidal flats of the north European Atlantic coast (e.g. Beukema and de Vlas 1979; Pollack 1979; Reise et al. 2001). There, the species covers about 70 % of c. 4,700 km² tidal flat area with an average density of 20–40 individuals per m² and is considered a structuring agent of regional landscape-forming processes (Beukema 1976; Riisgard and Banta 1998; Reise et al. 2010). In contrast, less is known about lugworm species in other regions of the world, including populations in small semi-enclosed tidal bays, where lugworms are less dominant and exhibit a more patchy distribution (Hobson 1967; Wilson 1981; Krager and Woodin 1993; Goerlitz et al. 2013). Previous studies have shown that lugworm distribution in tidal bays can be limited to certain locations on the shore, which has been associated with changes in habitat type, e.g. sediment vegetation, or hydrodynamic disturbance (Hobson 1967; Swinbanks and Murray 1981).

In southeastern New Zealand, the lugworm *Abarenicola affinis* (Ashworth 1903) is common in tidal inlets and estuaries, where it co-occurs with the seagrass *Zostera muelleri* (Irmisch ex Ascherson 1867) in a number of habitats (Wells 1963; Leduc et al. 2006; Goerlitz et al. 2013). *Zostera muelleri* is a short-bladed seagrass (5–15 cm blade length), which is common on intertidal flats throughout New Zealand, where it often exhibits a patchy distribution (Turner 2007). *Zostera muelleri* also has dense below-ground structures that may adversely affect macrofauna, including large bioturbators (van Houte-Howes et al. 2004; Berkenbusch et al. 2007). On the Otago coast, southeastern New Zealand, two adjacent tidal inlets are populated by *A. affinis* but differ in the occurrence of seagrass, with one inlet containing large areas of fragmented and continuous seagrass habitat, and the other inlet containing no seagrass. This difference in sediment vegetation between the two inlets was used in the present

study to examine the distribution, abundance, body size and biomass of *A. affinis* in seagrass and unvegetated habitats. The study assesses whether the presence of seagrass has an effect on the measured lugworm parameters in these habitats.

Materials and methods

Lugworm sampling

The study was carried out in two neighbouring tidal inlets in southeastern New Zealand, Papanui and Hoopers inlets (Fig. 1). Both inlets are of similar size (c. 4 km²) and have semidiurnal tides, with mean tidal ranges of 1.15 and 0.43 m, respectively (Albrecht and Vennell 2007). Whereas lugworms inhabit both inlets, seagrass only occurs in Papanui Inlet, but not in Hoopers Inlet. In Papanui Inlet, *Z. muelleri* forms an extensive, continuous meadow in the mid and low intertidal zones, whereas the high intertidal zone is characterised by fragmented seagrass habitat (Mills and Berkenbusch 2009).

Field sampling was carried out in four consecutive seasons, in summer (December) 2007, autumn (March), winter (June) and spring (September) 2008. In each inlet, an intertidal sampling area of 0.4 km² was selected, representing seagrass (Papanui Inlet) and unvegetated habitat (Hoopers Inlet). Both sampling areas included c. 600–700 m of intertidal area from the shoreline to the mean low tide water mark. Each sampling area was divided by a grid of 90 sampling points, and the position of points and their distance to the shoreline were established by global positioning system (GPS). In both sampling areas, distance from the shoreline corresponded with low tide exposure time ranging between 2 and 9 h per semidiurnal tidal cycle (visually assessed over 12 h). Based on these observations, distance from the shoreline was used as a proxy for tidal level. In both seagrass and unvegetated habitat, 15 sampling points were randomly chosen each season and sampled by collecting a sediment core (20 cm diameter or 314 cm² area to 40 cm depth). Each sampling core was extracted using a shovel and divided into 10-cm depth sections, which were individually sieved on 1-mm mesh. For each core and depth section, the collected lugworm were transferred into seawater containers for transportation.

In the laboratory, lugworms were anaesthetised for 3 h in 7 % magnesium chloride, fixed in 4 % formalin and subsequently preserved in 70 % ethanol. Following preservation, total and thorax lengths of lugworms were measured with calipers (± 0.5 mm). To determine ash-free dry weight (AFDW, ± 0.0001 g), lugworms were dried

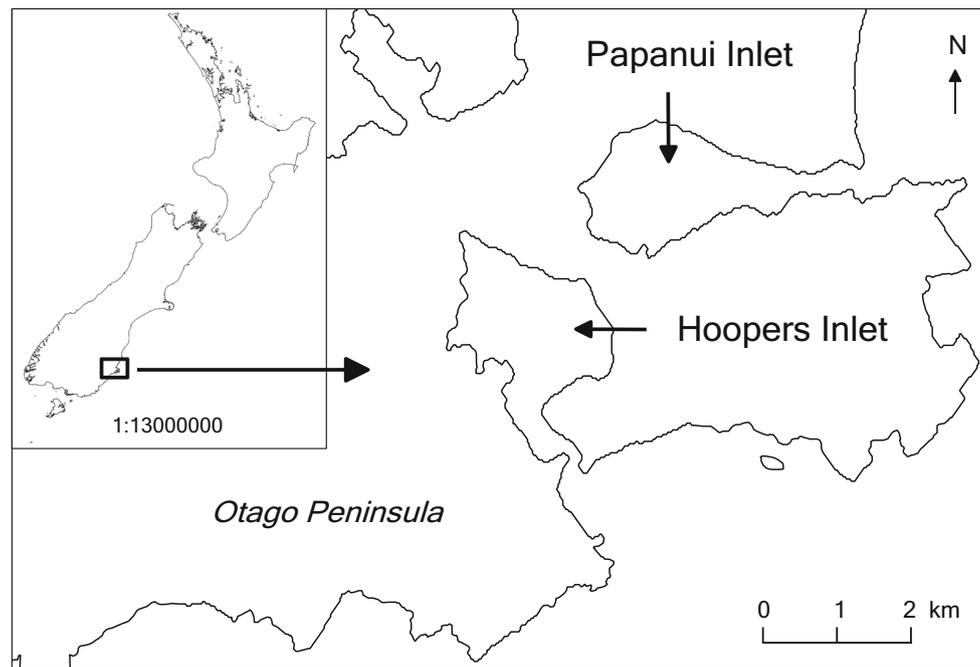


Fig. 1 Location of the intertidal seagrass (Papanui Inlet) and unvegetated (Hoopers Inlet) habitats in southeastern New Zealand

to constant weight (60 °C, 48 h) and combusted (500 °C, 4 h).

Habitat sampling

At each sampling point, two sediment cores were collected. The first core (4.7 cm diameter, 10 cm depth) was split for sediment granulometry and organic matter content analyses. The second core (2.5 cm diameter, 2 cm depth) was taken for sediment chlorophyll *a* analysis. The latter two parameters indicate potential food sources for lugworms in the form of available organic material (including seagrass detritus) and microphytobenthos (Longbottom 1970; Leduc et al. 2006; Widdows et al. 2008). In addition, in the seagrass habitat, seagrass within the lugworm sampling core was cut off at the sediment surface prior to excavation and retained. Seagrass roots, rhizomes and debris in the top 10-cm depth section of the core were subsequently collected during sieving.

In the laboratory, seagrass leaves, roots, rhizomes and debris were rinsed with freshwater, dried (60 °C, 48 h) and weighed (± 0.001 g). Sediment samples were wet-sieved to extract the fines fraction (< 63 μm), dried (60 °C, 48 h) and mechanically sieved to determine grain size fractions (63, 125, 250, 500, 1,000 μm) (McManus 1988). Organic matter content was determined by loss on ignition (500 °C, 4 h) (Buchanan and Kain 1971). Sediment chlorophyll *a* samples were freeze-dried (-50 °C, 48 h), homogenised, boiled in 90 % ethanol and analysed using a spectrophotometer (Sartory 1982).

Data analysis

Statistical analyses were conducted with STATISTICA 6.0 (StatSoft 2001) using a significance level of $P < 0.05$ for all tests. Examined *A. affinis* parameters were abundance, thorax length and biomass. Thorax length was selected instead of total length due to the occasional occurrence of incomplete worm tails. One-way ANOVA (Underwood 1997) was applied to test for differences in lugworm parameters across seasons within each habitat and for differences in lugworm parameters between habitats, combining data from all seasons. Data were tested for normality and homogeneity of variances by Kolmogorov–Smirnov and Cochran tests, respectively (Underwood 1997). Non-normally distributed data were accepted due to ANOVA’s robustness against non-normality (Underwood 1997). When necessary, data were square-root or \log_{10} -transformed to achieve homogeneity of variances. Although lugworm abundance data between habitats remained heterogeneous after transformation, ANOVA was considered reliable because test results were non-significant (heterogeneity only compromises the outcome of ANOVA when test results are significant, Underwood 1997). Between both habitats, *A. affinis* occurred in the size range 17–90 mm thorax length. Therefore, the size frequency distribution of *A. affinis* within each habitat was evaluated by categorising lugworms into eight arbitrary size classes: 11–20, 21–30, 31–40, 41–50, 51–60, 61–70, 71–80 and 81–90 mm thorax length.

In both the seagrass and unvegetated habitat, multiple linear regressions (Quinn and Keough 2002) were used to analyse the relationship between lugworm distribution and habitat variables, and data were combined across all seasons to assess general patterns. *Abarenicola affinis* abundance and biomass were used as dependent variables. Predictor variables included distance from the shoreline, sediment mean grain size and proportion of fines, and organic matter and chlorophyll *a* contents. In the seagrass habitat, seagrass above- and below-ground (roots, rhizomes and debris in the top 10 cm of sediment) biomasses were also included. Prior to analysis, *A. affinis* abundance and biomass data were $\log_{(x+1)}$ -transformed to improve residuals' normality and homogeneity of variances (graphically assessed by probability plots and plots of residuals against predicted values, respectively, Quinn and Keough 2002). Co-correlations were graphically assessed by matrix plots (Quinn and Keough 2002), leading to the omission of sediment mean grain size and seagrass above-ground biomass from the regression analysis in the seagrass habitat due to high correlation ($R^2 > 0.5$, $P < 0.001$) with proportion of fines and seagrass below-ground biomass, respectively.

Results

Lugworm characteristics in seagrass and unvegetated habitats

In both seagrass and unvegetated habitats, *A. affinis* showed little seasonal variation in mean values of abundance, thorax length and biomass (Table 1). In the seagrass habitat, lugworm abundance was greatest in autumn, compared with summer in the unvegetated habitat. In both types of habitat, lugworm biomass peaked in autumn. Results from

one-way ANOVA showed that differences in lugworm abundance, thorax length and biomass across seasons were not significant in either habitat (Table 2).

The two habitat types had a similar mean abundance of lugworms, but individuals were noticeably larger in the unvegetated habitat, resulting in greater biomass (Table 1). These differences were consistent across all seasons (and most pronounced in autumn) and were reflected by maximum total lengths and biomasses of lugworms in each habitat (Seagrass habitat: 110 mm; 0.0971 g AFDW, unvegetated habitat: 175 mm; 0.3982 g AFDW). Results from one-way ANOVA revealed no significant differences in lugworm abundance between habitats, but significantly greater thorax length and biomass of *A. affinis* in unvegetated habitat compared to seagrass habitat (Table 2).

Size frequency distributions of *A. affinis* showed that the two types of habitats were populated by lugworms with different ranges of size classes (Fig. 2). In relation to all size classes occupied in each habitat, medium-sized lugworm dominated in both habitats in three of four seasons (Fig. 2). In the seagrass habitat, lugworms occurred only in four smaller size classes with a noticeable peak in the size class 21–30 mm thorax length in autumn. In contrast, in the unvegetated habitat, larger individuals occurred in all seasons, whereas small lugworms (<40 mm thorax length) were generally less abundant compared with the seagrass habitat. In both habitats, the largest individuals were scarce in winter.

In both seagrass and unvegetated habitats, lugworm abundance and body size increased with increasing burrowing depth. Consequently, the differences in *A. affinis* body size between the two habitats resulted also in different burrowing depths (Fig. 3). In the seagrass habitat, lugworms did not occur below 30 cm depth. In contrast, lugworms in the unvegetated habitat showed their greatest abundance at 30–40 cm depth. These

Table 1 *Abarenicola affinis* abundance and biomass (per 314 cm² core; mean values \pm SD, $n = 15$), and thorax length (mean values \pm SD, $n = 19$ –31) in summer, autumn, winter and spring

Habitat type	Season	No. of sampling cores	No. of individuals	Mean abundance \pm SD	Mean thorax length (mm) \pm SD	Mean biomass (g AFDW) \pm SD
Seagrass (Papanui Inlet)	Summer	15	21	1.4 \pm 1.4	31.2 \pm 8.6	0.033 \pm 0.047
	Autumn	15	29	1.9 \pm 2.5	27.4 \pm 5.4	0.047 \pm 0.063
	Winter	15	20	1.3 \pm 1.9	30.0 \pm 6.3	0.033 \pm 0.050
	Spring	15	19	1.3 \pm 1.4	31.0 \pm 7.4	0.045 \pm 0.068
	Overall	60	89	1.5 \pm 1.8	29.6 \pm 6.9	0.040 \pm 0.056
Unvegetated (Hoopers Inlet)	Summer	15	31	2.1 \pm 1.5	43.4 \pm 10.5	0.107 \pm 0.122
	Autumn	15	22	1.5 \pm 1.1	47.6 \pm 13.8	0.163 \pm 0.118
	Winter	15	21	1.4 \pm 1.1	41.9 \pm 11.8	0.101 \pm 0.086
	Spring	15	22	1.5 \pm 1.2	43.6 \pm 14.7	0.100 \pm 0.077
	Overall	60	96	1.6 \pm 1.2	44.1 \pm 12.5	0.118 \pm 0.102

(December 2007, March, June, September 2008, respectively) in seagrass and unvegetated habitat

Table 2 Results of one-way ANOVA (factor season) for *Abarenicola affinis* abundance and biomass (per 314 cm² core; *n* = 15), and thorax length (*n* = 19–31) in seagrass and unvegetated habitat, and

results of one-way ANOVA (factor habitat) (*n* = 60 for abundance and biomass; *n* = 89/96 for thorax length, all seasons) (significant values in bold)

<i>Abarenicola affinis</i> parameters	Seasonal comparison						Habitat comparison		
	Seagrass			Unvegetated			<i>df</i>	<i>F</i>	<i>P</i>
	<i>df</i>	<i>F</i>	<i>P</i>	<i>df</i>	<i>F</i>	<i>P</i>			
Abundance	3	0.41	0.750	3	0.98	0.410	1	0.17	0.682
Thorax length (mm)	3	1.63	0.190	3	0.82	0.489	1	101.37	<0.001
Biomass (g AFDW)	3	0.28	0.837	3	1.31	0.280	1	30.44	<0.001

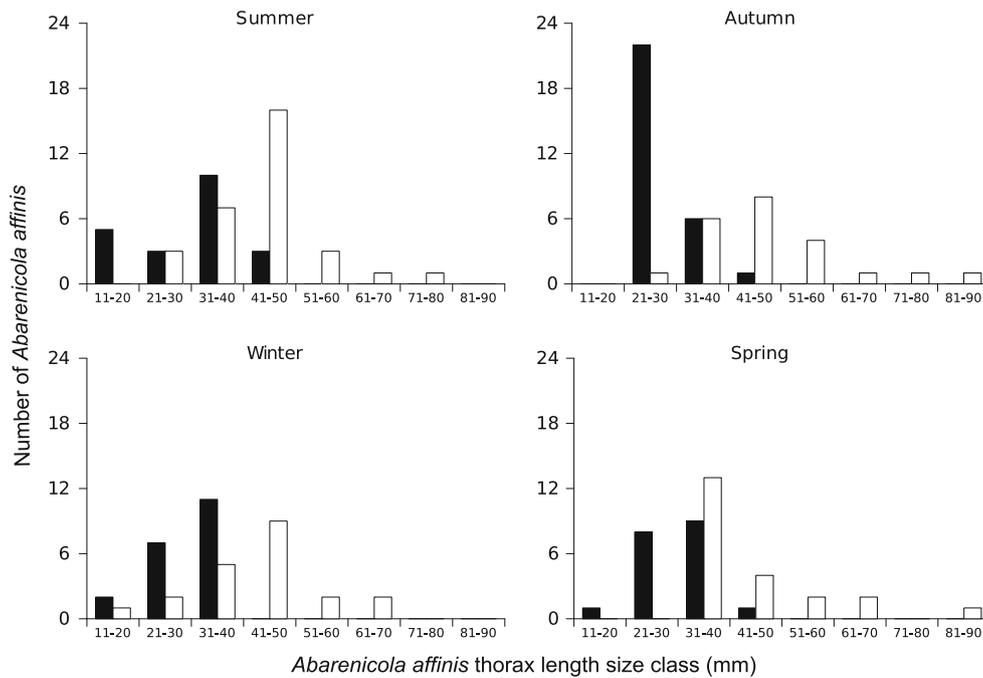


Fig. 2 Size frequency distributions of *Abarenicola affinis* in summer, autumn, winter and spring (December 2007, March, June, September 2008, respectively) in seagrass (filled bars *n* = 21, 29, 20, 19, respectively) and unvegetated habitat (open bars *n* = 31, 22, 21, 22, respectively)

findings were reflected in the markedly greater mean burrowing depth of lugworms in the unvegetated habitat [32.7 ± 7.8 (SD) cm, *n* = 96] compared with the seagrass habitat (23.6 ± 6.9 cm, *n* = 89).

Lugworm distribution in seagrass and unvegetated habitats

Both habitats had relatively similar sediment types with mean sediment grain sizes of 145 ± 6 (SD) μ m in seagrass habitat and 148 ± 1 μ m in unvegetated habitat (both *n* = 60, data from all seasons). At the same time, sediment was muddier in the seagrass habitat, as evident in the higher proportion of fines of 4.15 ± 2.51 % (SD) (maximum 13.2 %) compared with 2.11 ± 0.57 % (maximum 3.6 %) of fines in the unvegetated habitat. Organic matter content was relatively low in both habitat types at

0.64 ± 0.13 % (SD) and 0.55 ± 0.09 % in the seagrass and unvegetated habitat, respectively. The other food variable, microphytobenthos measured as chlorophyll *a* content, was higher in the unvegetated habitat, with 5.0 ± 2.3 (SD) μ g chlorophyll *a*/g sediment dry weight compared with 3.7 ± 1.4 μ g chlorophyll *a*/g sediment dry weight in the seagrass habitat (*n* = 60, all seasons). In the seagrass habitat, *Z. muelleri* above-ground and below-ground biomasses were on average 0.143 ± 0.148 (SD) g dry weight and 3.833 ± 2.486 g dry weight, respectively (*n* = 60, all seasons).

In the seagrass habitat, the distribution of *A. affinis* was significantly influenced by habitat variables, as revealed by multiple linear regression analysis (Table 3). The combination of measured habitat variables explained 68 and 71 % of the variation in lugworm abundance and biomass, respectively. Semi-partial correlation coefficients, which

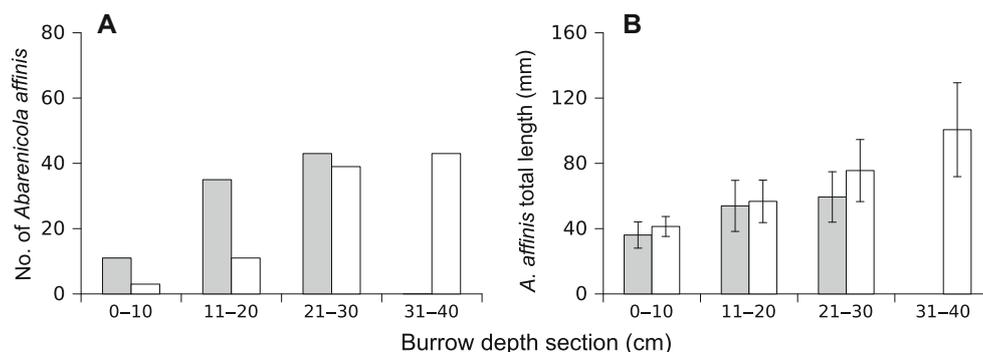


Fig. 3 Total number (a) and total length (b) of *Abarenicola affinis* (mm, mean values \pm SD, $n = 3$ –43) per burrow depth section in seagrass (shaded bars) and unvegetated habitat (open bars), sampled between summer 2007 and spring 2008

Table 3 Results of multiple linear regression analyses of *Abarenicola affinis* abundance and biomass and habitat variables in seagrass and unvegetated habitat (all seasons combined, $n = 60$) (significant values in bold; R^2_{sempart} = squared semi-partial correlation coefficient,

indicating the proportion of variance explained by the inclusion of the predictor variable)

Habitat type	<i>Abarenicola affinis</i> abundance			<i>Abarenicola affinis</i> biomass			
	<i>F</i>	<i>R</i> ²	<i>P</i>	<i>F</i>	<i>R</i> ²	<i>P</i>	
Seagrass	22.75	0.678	<0.001	26.93	0.714	<0.001	
Unvegetated	0.90	0.077	0.490	0.94	0.080	0.464	
<i>Seagrass habitat</i>		<i>F</i>	<i>R</i> ² _{sempart}	<i>p</i>	<i>F</i>	<i>R</i> ² _{sempart}	<i>p</i>
Seagrass below-ground biomass (g dry weight)		4.87	−0.170	0.032	6.57	−0.187	0.013
Distance from the shoreline (m)		39.09	−0.483	<0.001	20.29	−0.328	<0.001
Sediment proportion of fines (%)		1.62	0.010	0.209	12.42	0.257	<0.001
Organic matter content (%)		0.36	0.046	0.553	0.72	0.062	0.400
Chlorophyll <i>a</i> content (μg/g sediment dry weight)		0.29	−0.041	0.596	0.17	−0.030	0.684

indicate the relative importance of each variable, were significant for seagrass below-ground biomass and distance from the shoreline; both variables were negatively related to *A. affinis* abundance and biomass. In addition, the proportion of fines was significantly positively related to *A. affinis* biomass only, revealing an increase in average lugworm size with increasing proportion of fines in the sediment. By contrast, the measured habitat variables did not explain lugworm distribution in Hoopers Inlet (Table 3).

The distribution patterns of *A. affinis* in seagrass and unvegetated habitats support the findings of the multiple regression analyses (Fig. 4). In the seagrass habitat, lugworm abundance showed a distinct zonation pattern with respect to distance from the shoreline and the distribution of seagrass. Lugworm abundance was highest in the upper intertidal zone (within 100 m from the shoreline) and declined with distance from the shoreline. At the same time, seagrass below-ground biomass showed an increase from relatively low levels in the upper intertidal zone to the highest values at about 250–450-m distance from the shoreline. In these lower intertidal areas where seagrass

biomass was high, lugworm abundance was greatly reduced. A marked decline in lugworm abundance occurred at about 150-m distance from the shoreline, where seagrass showed a considerable increase in below-ground biomass. In contrast, in unvegetated habitat, lugworm abundance was relatively evenly spread throughout the intertidal area, with no clear pattern evident in relation to distance from the shoreline (Fig. 4).

Given the significant influence of seagrass biomass, distance from the shoreline and the proportion of fines on *A. affinis* distribution in the seagrass habitat, the spatial variation of lugworm size classes in relation to these habitat variables was assessed. The range of each variable was compared across different lugworm size classes, including all samples containing lugworms of the respective size class (Table 4). Whereas the largest *A. affinis* populated unvegetated areas in the high intertidal zone, where sediment contained the highest proportion of fines, medium-sized lugworms occurred in areas that had no or low seagrass biomass, with a variable proportion of fines and variable distances from the shoreline. The smallest

individuals (11–20 mm thorax length) colonised areas of markedly greater seagrass biomass than medium- and large-sized individuals; they also showed a similar distribution across the shore as medium-sized lugworms, but did not occur in the muddiest sediment of this habitat.

Discussion

Lugworm characteristics in seagrass and unvegetated habitats

In both habitat types, *A. affinis* showed no marked changes in overall abundance through the year, suggesting temporal stability in the lugworm populations of these habitats. One

important aspect of this study, however, is that the focus was on adult lugworms, and the sampling design did not include juvenile worms. Furthermore, the generally low population density of *A. affinis* in southern New Zealand (e.g. compared with *A. marina* in north European tidal bays, Reise et al. 2001; Goerlitz et al. 2013) meant that individual numbers were low. Whereas previous studies have shown that lugworm populations are characterised by temporal stability (Flach and Beukema 1994), seasonal variation may occur, e.g. due to mortality and migration of adult worms into subtidal locations (Reise et al. 2001). In the present study, these kinds of pattern were not evident, but a different sampling design, including the targeting of juvenile worms, is required to elucidate seasonal dynamics in the *A. affinis* populations.

Although overall abundances were similar in both habitats, lugworms in the seagrass habitat were smaller and had significantly lower biomass compared with lugworms in the unvegetated habitat (also resulting in markedly greater burrowing depth of *A. affinis* in the latter habitat). The size distributions of *A. affinis* indicated a general difference between the two habitats with a greater number of small lugworms and a noticeable lack of large individuals in the seagrass habitat compared with the unvegetated habitat. This difference could originate from different growth and longevity of *A. affinis* between the two habitats, but size–age relationships are unknown for this species. Lugworm growth rates depend on external factors such as food availability (Linton and Taghon 2000). In the present study, sediment organic content was similarly low in both habitat types, whereas microphytobenthos abundance (measured as sediment chlorophyll *a* concentration) was higher in the unvegetated habitat than in the seagrass habitat. In contrast to other studies that have documented increased organic matter accumulation and microphytobenthos growth in seagrass areas due to attenuation of water flow (Widdows et al. 2008), these effects appear to be less distinct in the seagrass habitat of the present study. As detritus of *Z. muelleri* represented an additional available food source for *A. affinis* (Leduc et al. 2006), food availability was not considered to be a limiting factor for lugworm growth in the seagrass habitat.

Sampling in the present study did not detect any lugworm >50 mm thorax length in Papanui Inlet, and it

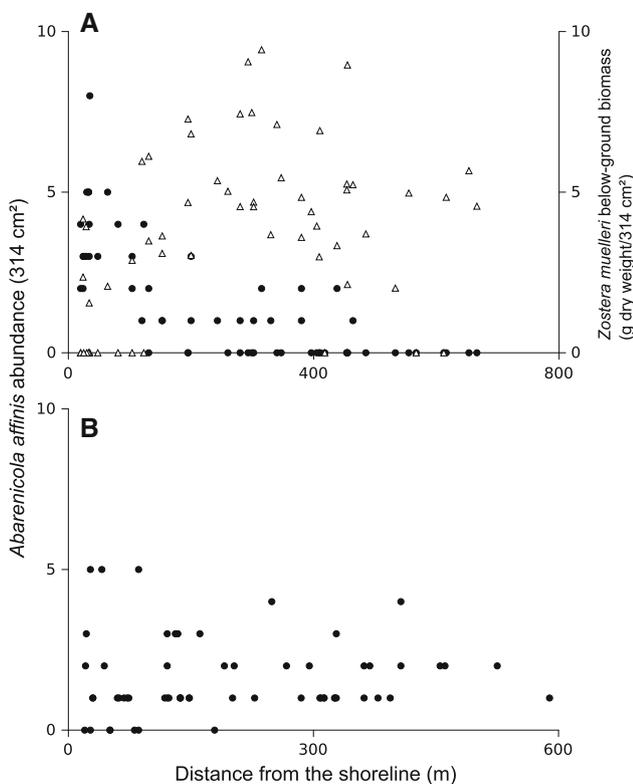


Fig. 4 *Abarenicola affinis* abundance (filled circle) and *Zostera muelleri* below-ground biomass (triangle) and distance from the shoreline in seagrass (a) and unvegetated (b) habitat. Data combined from seasonal sampling between summer 2007 and spring 2008

Table 4 *Abarenicola affinis* size classes and habitat variables in seagrass habitat. Data combined from seasonal sampling between summer 2007 and spring 2008

Thorax length (mm)	No. of individuals	Seagrass below-ground biomass (g dry weight)	Distance from the shoreline (m)	Proportion of fines (%)
11–20	8	2.356–6.815	24–380	2.6–7.2
21–30	40	0–9.433	20–380	2.2–13.2
31–40	36	0–9.433	20–464	4.0–13.2
41–50	5	–	20–81	6.3–13.2

remains unknown whether individuals of this thorax length are absent from the *A. affinis* population in this inlet. The lack of large individuals in a lugworm population may be associated with premature mortality or adult migration into subtidal locations (Lackschewitz and Reise 1998; Reise et al. 2001). In the present study, there was no evidence of either pattern. Throughout the sampling, no dead adults were observed on the tidal flat and, there has been no report of *A. affinis* from subtidal regions off the Otago coast to date. The noticeable peak in the number of small individuals (i.e. 21–30 mm thorax length) in autumn in the seagrass habitat may be the result of post-juvenile recruitment as data derived from gamete observations on *A. affinis* indicate that individuals <20 mm thorax length do not carry gametes in their coelomic fluid, i.e. they are immature (S. Goerlitz unpubl. data). Concentrations of small lugworms in seagrass habitat have been also documented from north European tidal flats (*A. marina* in *Zostera marina* beds, Reise 1985). Similarly to its European counterpart, small *A. affinis* may use the above-ground vegetation of *Z. muelleri* as shelter from predation and environmental stresses.

Lugworm distribution in seagrass and unvegetated habitats

None of the measured habitat variables explained the lugworm distribution in unvegetated habitat, whereas the distribution of *A. affinis* was significantly related to the distribution of *Z. muelleri*, distance from the shoreline and proportion of sediment fines (lugworm biomass only) in the seagrass habitat. In this habitat, below-ground biomass had a significant negative influence on abundance and biomass of *A. affinis*. At the same time, other habitat variables such as organic matter content and sediment composition were relatively similar between seagrass and unvegetated habitat. These findings indicate that seagrass had a limiting effect on lugworm distribution in an otherwise suitable habitat.

The negative influence of seagrass on lugworm distribution is most likely caused by a reduced burrowing mobility of *A. affinis* within the root structures of *Z. muelleri*, which are difficult to penetrate for large bioturbators (Berkenbusch et al. 2007). The *Z. muelleri* bed in Papanui Inlet has established an extensive root-rhizome matrix below the sediment surface, and the measured below-ground biomass was comparable to that of other studies documenting impacts of seagrass root mats on macrofaunal distribution in tidal flats (Brenchley 1982; van Houte-Howes et al. 2004). Previous studies have shown that lugworms take considerably longer to re-burrow in seagrass compared with unvegetated sediment (Brenchley 1982). Also, irrigation and feeding activities of lugworms

depend on sediment permeability; hence, lugworm maintain permeable conditions to their own benefit when dominating habitats (Volkenborn et al. 2007). In contrast, the cohesive below-ground structures of seagrasses, such as in *Z. muelleri*, increase sediment compaction (Brenchley 1982; Siebert and Branch 2005; van Wesenbeeck et al. 2007), thus creating less suitable conditions for lugworm feeding activities. For example, headward irrigation by the lugworms, sitting at the lower end of its burrow, creates an upward flow of porewater and loosens the sediment, resulting in a sinking column of particles, on which lugworm feed on (Riisgard and Banta 1998). This process could be severely hampered by seagrass roots, binding the sediment together.

The zonal distribution of *A. affinis* in the seagrass habitat, i.e. the steady decrease in abundance towards the middle of the tidal flat, where seagrass below-ground biomass showed maximum values, suggested that lugworms were more affected by the dense structures within the seagrass bed than at the margin of the bed. This edge effect may arise from a threshold level of below-ground biomass, above which lugworms colonise seagrass areas at lower abundances. A similar effect was reported for deep burrowing polychaetes in estuaries in northern New Zealand, with higher polychaete abundance outside and at the edges of *Z. muelleri* beds, compared with areas inside the beds, where seagrass biomass was highest (van Houte-Howes et al. 2004).

Apart from being spatially limited by the presence of the *Z. muelleri* bed, *A. affinis* may have concentrated in the high intertidal zone of Papanui Inlet due to less hydrodynamic disturbance in these upper shore areas compared with lower shore areas. An increase in hydrodynamic forces such as tidal currents and wave action in lower shore areas may result in unstable surface sediment, which has negative effects on lugworm burrow maintenance and feeding processes (Hobson 1967; Beukema and de Vlas 1979). A preference of *A. affinis* for sheltered habitats in near-shore areas has been suggested (Glasby et al. 2009). In the unvegetated habitat in Hoopers Inlet, hydrodynamic disturbance is presumably lower compared with Papanui Inlet due to the narrow entrance channel of the former inlet, resulting in less than half the tidal range and creating a shallow slow-flow environment (Albrecht and Vennell 2007). Therefore, lugworms in lower shore areas in the unvegetated habitat were not limited either by seagrass or by hydrodynamic forces, which may explain their relatively homogeneous distribution across all tidal levels in this habitat.

In the seagrass habitat, the largest *A. affinis* occurred in the finest sediment, which was in the high intertidal zone and coincided with unvegetated areas. The results suggest that an increase in the proportion of fines had an additional

positive effect on lugworm sizes in this habitat; however, it seems unlikely that this was the case, as lugworms in the unvegetated habitat were considerably larger than the largest individuals in the seagrass habitat, but sediment was relatively coarser compared with the seagrass habitat.

In the seagrass habitat, intertidal areas with greater seagrass biomass contained only the smallest individuals. Small lugworms may be less restricted in their burrowing and feeding activities by seagrass root-rhizome systems compared with larger individuals (Brenchley 1982). In contrast, the limited space of unvegetated sediment in the seagrass habitat seemed to confine larger lugworms in their spatial distribution and may be, in part, responsible for the lack of individuals as large as in the unvegetated habitat. The findings indicate the potential of *Z. muelleri* to influence the spatial distribution of different size classes of *A. affinis* in seagrass-unvegetated habitat mosaic.

In summary, the present study highlights the negative feedback of seagrass on lugworms, whereas other studies have shown mutual negative effects or have emphasised the negative influence of lugworms on the distribution of seagrass in tidal flats (Phillipart 1994; Valdemarsen et al. 2010; Suykerbuyk et al. 2012). Where lugworms and seagrasses co-occur, their opposing ways of modifying the sediment may result in the potential of each ecosystem engineer to prevent the establishment of the other type of engineer (van Wesenbeeck et al. 2007). The present study indicated that such interactions play a role in the variation of lugworm distribution and body size among tidal inlets of southern New Zealand; an established seagrass bed restricted the spatial extent of *A. affinis*, particularly of large individuals, in an otherwise suitable habitat. Given the potential of lugworms to adversely affect seagrass distribution (Phillipart 1994; Suykerbuyk et al. 2012), future research is needed to elucidate factors determining the predominance of either type of organism in joint habitats, as well as factors that may cause shifts in their distributions.

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